THE ABUNDANCE AND DISTRIBUTION OF MEGAFAUNAL MARINE INVERTEBRATES IN RELATION TO FISHING INTENSITY

OFF CENTRAL CALIFORNIA

By

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Abstract

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Deep-water megafaunal invertebrates such as corals and sponges contribute to biodiversity, create fish habitat, and can indicate long-term environmental conditions. These structurally complex invertebrates are easily damaged by commercial and recreational fishing gear. This impact is of particular concern because the long-term viability of fish populations may be threatened by habitat degradation, specifically the removal and destruction of structureforming invertebrates. This study examines the abundance and distribution of megafaunal invertebrates on the continental shelf at three sites within the Monterey Bay National Marine Sanctuary, CA. Each site (Portuguese Ledge, Point Sur, and Big Creek) has been subjected to varying levels of fishing effort and gear use. Of particular interest were the effects of fishing to the abundance of megafaunal invertebrates categorized as slow-growing, sessile species and fastgrowing, mobile species. The level of fishing disturbance to these two biologically different groups of invertebrates was predicted to vary based on the magnitude, areal extent, and frequency of each bottom-contact fishing gear. Underwater video surveys, conducted in the

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1990s using the *Delta* submersible, were used to describe habitat and quantify invertebrates. A total of 54,439 individual invertebrates from 54 taxa were documented on high-relief rock and soft sediment habitats among the three sites. Overall, there were little to no detected effects on invertebrates due to fishing. Environmental variables are most likely influencing invertebrate abundance and distribution. The documentation of invertebrates at these sites is important because they are within newly established marine protected areas. These historical data will serve as a reference point for future monitoring of the sites in terms of how habitat conditions and invertebrate abundances have benefited from the implementation of new management regulations.

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INTRODUCTION

Fishing has a range of ecological impacts to marine habitats, depending on the type of gear, spatial extent, and frequency of fishing effort (Auster and Langton, 1999). Of particular interest are the effects of bottom-contact fishing gear on megafaunal benthic invertebrates found in continental shelf and slope ecosystems (Dayton et al., 2002; Morgan et al., 2005; Hixon and Tissot, 2007). Megafaunal invertebrates (generally >5cm in height) contribute to biodiversity, provide habitat for fishes and other invertebrates, and can be indicators of long-term environmental conditions (e.g. Brusca and Brusca, 1990; Krieger and Wing, 2002; Tissot et al., 2006). Specifically, megafaunal invertebrates such as deep sea corals and sponges can be sessile, slow-growing, long-lived, and fragile (Leys and Lauzon, 1998; Andrews et al., 2002), making them vulnerable to damage by fishing gear that make contact with the seafloor (Freese, 2001; Krieger, 2001; Dayton et al., 2002; Fossa et al., 2002; Rogers, 2004; Hourigan et al., 2007). Dense aggregations of other megafaunal invertebrates, such as echinoderms (crinoids and sea stars), may enhance the structural component of fish habitat (Tissot et al., 2006). These species are mobile and fast-growing, possibly making them more resilient than corals and sponges to impacts from bottom-contact fishing gear (e.g. Freese et al., 1999; Hixon and Tissot, 2007).

The degree of damage to megafaunal invertebrates by fishing gear is dependent on how the gear is used. For example, characterizing ecological disturbances (e.g. Sousa, 1984) of fishing gear consists of three components: (1) the magnitude (intensity and severity) of gear impact, (2) the spatial extent of the impacted area is dependent on if the gear is towed continuously across the seafloor or contacts the bottom at limited points, and (3) the frequency of gear use per unit time (Morgan and Chuenpagdee, 2003).

Bottom trawling poses the greatest threat to megafaunal invertebrate communities due to both the extensive contact and substantial forces of the gear on the seafloor per haul, the duration of the haul, and (in many places) a high frequency of use (Watling and Norse, 1998; NRC, 2002). Bottom trawl gear is primarily towed over level mud-sand sediments or low-relief rocky areas (facilitated by roller gear), resulting in the removal, crushing, and burying of structurally complex megafaunal invertebrate taxa that are associated with these habitats (Auster et al., 1996; Freese, 2001; NRC, 2002).

Similarly, the severity of damage to megafaunal invertebrates from the deployment and hauling of traps is substantial. Traps are typically fished on soft sediments and can crush or snag invertebrates living on these habitats (Freiwald et al., 2004). Further, if traps are dragged long distances during retrieval, the force and spatial extent of disturbance to the seafloor and sessile megafaunal invertebrates greatly increases. Frequency of disturbance to megafaunal invertebrates is greater with the use of longline traps (10-90 traps strung together) than the impact of single-set traps (Valdemarsen and Suuronen, 2001; Morgan and Chuenpagdee, 2003).

Although the direct effects of bottom-set gillnets and longlines to benthic communities are not well known, these gears can become entangled on high-relief or irregular rocky bottoms and consequently damage or remove megafaunal invertebrates (Valdemarsen and Suuronen, 2001; Morgan and Chuenpagdee, 2003; Freiwald et al., 2004). During gear employment, the areal extent of the seafloor disturbed by set gillnets and longlines is limited to the weights used to anchor the gear. However, a National Marine Fisheries Service (NMFS) study off the southeast coast of Alaska observed habitat damage caused by halibut longline gear and found that it was during the retrieval process that the line swept a considerable distance over the seafloor and caused the most damage to corals and other invertebrates (NMFS, 1998). Similar

impacts would most likely occur if set gillnets were to make contact with the seafloor during retrieval. Further, the frequency of disturbance is magnified by the hundreds to thousands of hooks attached to each longline and the large sizes of one gillnet (up to 450m long), as these features increase the possibility that these gears will become entangled on structurally complex megafaunal invertebrates.

Very little information exists concerning the direct impacts to megafaunal invertebrates from hook and line fishing, a popular and efficient method for recreational anglers in rocky reef areas. Sinkers and monofilament line that make contact with the seafloor can damage and become entangled on fragile corals and other sessile species (Morgan and Chuenpagdee, 2003; Whitmire and Clarke, 2007). Although the magnitude and areal extent of impact may be small for an individual line, the high density and frequency of recreational anglers in some areas could result in significant impacts.

Over the past century, the fishing industry has seen many technological advances of fishing gear to enhance overall catch per fishing trip. Yet as the intensity of fishing increases, so do the potential components of disturbance to seafloor habitats and the associated megafaunal invertebrates. This paper evaluates the potential levels of impact of bottom-contact fishing gear on two categories of megafaunal invertebrates. The first category includes structurally complex, slow-growing, and sessile species such as sponges, gorgonians, and sea pens. Soft-bodied, fast-growing, and mobile species like sea stars and crinoids comprise the second category. The impacts of bottom fishing gear to these two groups of invertebrates are dependent on their biological characteristics, the habitats they live in, and the disturbance components of each gear type (Table 1).

Potential impact levels (high, moderate, low) to the two categories of invertebrates were predicted using a synthesis of reported fishing gear disturbances to invertebrates, while also accounting for the three components of fishing gear disturbance (Table 2). The level of impact to these two categories of invertebrates by fishing gear is described in terms of decreasing their overall abundance and size. Bottom trawling can potentially have the greatest impact to slowgrowing, sessile, and structurally erect megafaunal invertebrates that live in soft sediment and low-relief rock habitats that trawl fishers typically target (NRC, 2002; Hourigan et al., 2007). However, bottom trawling is likely to have a moderate impact to mobile, soft-bodied invertebrates, as these fast-growing species will be temporarily displaced and have faster recovery rates then corals and sponges (Freese et al., 1999; Hixon and Tissot, 2007). Traps are fished primarily on soft bottoms and will have a moderate impact to fragile, sessile megafaunal invertebrate species found in these habitats (Morgan and Chuenpagdee, 2003). In comparison, the overall level of impact to the soft-bodied, mobile invertebrate species caused by traps will be low. If bottom-set longlines and gillnets are set over high-relief rock habitats, they may have a moderate impact to the associated sessile, structurally complex megafaunal invertebrate species during gear retrieval (Morgan and Chuenpagdee, 2003; PFMC, 2005). On the other hand, the soft-bodied characteristics of mobile species will provide more resilience to the level of impact of these gear types. Also, if hook and line sinkers and monofilament line become entangled on rocky reefs, the impacts to the associated fragile, structurally complex megafaunal invertebrate species will be medium to low and most likely there will be low to no impact to mobile invertebrate species (Whitmire and Clarke, 2007) (Tables 1 and 2).

The goals of this study were to assess the distribution, density, and size of megafaunal invertebrates at three sites off central California's continental shelf within the Monterey Bay

National Marine Sanctuary in relation to geographic variability in fishing intensity. Each site (Portuguese Ledge, Point Sur, and Big Creek) varied in levels of fishing effort and until now, the invertebrate communities in these areas had never been officially documented. Therefore the specific objectives were to: (1) quantify the density and size distribution of megafaunal invertebrates according to depth and substratum type at each site; (2) evaluate spatially specific commercial and recreational fishing effort data by gear type and document derelict fishing gear at each site; and (3) compare the differences among sites in relation to predicted levels of fishing gear impacts to (a) slow-growing, sessile and (b) fast-growing, mobile megafaunal invertebrate species.

METHODS

Study Sites

Benthic habitats and megafaunal invertebrates were quantified at the three study sites using the occupied submersible *Delta* (Figure 1). First, Portuguese Ledge, a popular fishing spot in southern Monterey Bay (center point: 36°40'N, 121°58'W) was surveyed from 9-12 October 1993 (see Anderson and Yoklavich, 2007 for description of study). Geology of the Portuguese Ledge area is primarily granite rock outcrops and low-relief Monterey formation covered by fine mud sediment that is common in the surrounding areas of Monterey Bay (Eittreim et al., 2000). Water flow at depths greater than 25 meters within Monterey Bay is understood to be cyclonic circulation and the Monterey Submarine Canyon may contribute to upwelled waters found in the bay (Breaker and Broenkow, 1994). The second site, Point Sur, is a high-current, rocky reef area of metamorphic Franciscan complex (Eittreim et al., 2000) located off the coast of Big Sur (center point: 36°15'N, 121°59'W), surveyed 28 and 29 September 1994. The Big Creek Ecological Reserve (BCER), the third study site, is located along an exposed coast on a narrow

margin of the continental shelf that expands from shallow, high-surge kelp forests to deep-water submarine canyons at the outer extent. The Big Creek area is about 90 km south of Monterey and the reserve was closed to fishing in September 1994 (center point: 36°4'N, 121°37'W). The BCER was surveyed both inside and outside of reserve boundaries during 29 September–3 October 1997 and 20–24 September 1998 as part of a larger study assessing rockfishes (see Yoklavich et al., 2002 for description of study). The orientation of Point Sur and Big Creek along the West coast are in the direction of the prevailing northwesterly winds and cold water supplied by the California current create Ekman transport that results in nutrient rich upwelling events in these areas (Rosenfeld et al., 1994; Yoklavich, et al., 1997).

Habitat and Invertebrate Surveys

Seafloor maps of substratum types were used to select submersible dive sites at the three study areas for habitat and invertebrate surveys, between 19-252 m depth on hard to mixed rock and soft sediment habitats. Dives were conducted continuously during daylight hours and documented using a high-8-mm video camera externally mounted on the starboard side of the submersible. Each dive consisted of 1-4 10 or 15-minute transects about 1 m above the seafloor at a speed of 0.4-1.0 knots depending on currents and topography. Transect width was maintained approximately constant at 2 m and verified using a hand-held sonar gun from inside the submersible and two parallel lasers set 20 cm apart on either side of the external video camera. Measurements of habitat features and invertebrates were made by comparing the object to the known spacing of the two laser spots. The location of the submersible was tracked using an ORE Trackpoint II plus USBL system and navigational software. Final habitat and invertebrate data were derived from observations of videotapes conducted by the same person (K. Graiff) to eliminate between-observer variability.

Habitat types were determined using a combination of eight categories of substratum type developed from methods described in Stein et al. (1992). Substratum categories, in order of decreasing particle size and vertical relief, were: rock ridge (R), continuous flat rock (F), boulder (B), cobble (C), pebble (P), gravel (G), sand (S), mud (M). The substratum codes were used in a two-character coding system to quantify distinct changes in habitat type along the transect, thus creating "habitat patches" of uniform substratum type. The primary character in the code represented the substratum type that accounted for at least 50% of the patch, and the secondary character represented the substratum type that accounted for at least 20% of the patch (e.g., "RM" represented a patch with at least 50% cover by rock ridge and at least 20% cover by mud). Habitat patches less than 10-seconds in duration were not recorded as individual patches. The area of each habitat patch was determined by multiplying the transect width (2 m) by the length of the habitat patch as was determined from the distance between the beginning and end geographic position of each habitat patch.

Megafaunal invertebrates were identified to the lowest taxonomic level and enumerated within each habitat patch. Sponges were classified by general morphology (i.e., flat, foliose, barrel, and vase sponges). Gorgonians (order Gorgonacea) could not be accurately identified to species level, yet were most likely of the genera *Swiftia* and *Lophogorgia*. Densities of megafaunal invertebrates were estimated by dividing total species abundance for each taxa by the area of their associated habitat patches. For each large, slow-growing, and sessile invertebrate (such as corals and sponges) their maximum size was estimated and geographic position recorded. The frequency and type of derelict fishing gear was also documented and any damaged invertebrates were noted.

Habitat and Invertebrate Data Analysis

Of the 64 possible habitat combinations, 32 different habitat patches were documented across all submersible dives. A cluster analysis (Pearson distance, grouped average method) was used to pool the habitat patches into 16 distinctive types based on ≥80% similarity and using the abundance of the 13 most observed megafaunal invertebrate species. Habitat types were further categorized using the following groupings: high relief rock substrata (RR, RB, RS, RM) were categorized as "hard"; mixed cobble and boulder rock substrata (BB, BC, BS, CB, CM, SB) were grouped as "mixed"; and mud and sand dominated substrata (SC, SS, MR, MC, MS, MM) were combined into the category "soft".

Surveys at Big Creek were conducted relatively soon after the implementation of the reserve and considering the long-life histories of megafaunal invertebrates, there would be little to no differences in the invertebrate community inside versus outside of the reserve. Therefore, a preliminary correspondence analysis (CA) was used to explore patterns in the megafaunal invertebrate community and habitats on submersible dives conducted inside and outside of the Big Creek reserve boundaries. CA is a method that creates an ordination on the distances between row and column attributes of a two-way contingency table in a lower-dimensional display (see Greenacre, 1984). In this study, rows were habitat patches and columns were invertebrate species. A one-way analysis of variance (ANOVA) was used to test for differences in CA species scores inside versus outside Big Creek reserve boundaries. Overall, the abundance and distribution of megafaunal invertebrates were not significantly different on either dimension 1 scores (F=0.72; df=1, 504; p=0.398) or dimension 2 scores (F=1.32; df=1, 504; p=0.251) and these two areas were pooled for subsequent analyses. Furthermore, data from the two sampling

years (1997 and 1998) were pooled and submersible dives re-surveyed in 1998 were not included in any of this study's analyses.

Nonmetric Multidimensional Scaling (NMDS) ordination was used to examine the community structure of slow-growing, sessile and fast-growing, mobile megafaunal invertebrates among habitats at the three sites. The slow-growing, sessile species included flat, foliose, barrel, and vase sponges, gorgonians, and Subselliflorae sea pens. Fast-growing and mobile invertebrates included many species and the analysis focused on the taxa that were most common at all sites, such as crinoids (Florometra serratissima) and vermillion sea stars (Mediaster *aequalis*). NMDS iteratively searches for the best positions of *n* entities on *k* dimensions (axes) with minimal stress of the k-dimensional configuration. "Stress" is a measure of departure from monotonicity in the relationship between the distance of the original data and the distance in the final ordination. Sorenson's (Bray-Curtis) distance measure was used and the ordination that most adequately described the data was chosen based on the final stress in relation to the dimensionality. Points on the ordination that were closer together represented the sites and habitats that were similar in invertebrate composition versus points that were farther apart. All data were $\log_{10}(x+1)$ transformed and multivariate analyses were conducted in PC-ORD 5.10 (McCune and Mefford, 1999).

Fisheries Data Collection

To document fishing intensity by gear type at each site for the range of years of the submersible surveys (1993-1998), the history of regulatory changes in the region were reviewed and commercial and recreational logbook data were obtained. Bottom trawling was prohibited in 1953 within three nautical miles of California's shoreline (state waters) (Haugen, 1990). In 1986, it became unlawful to use gillnets to take rockfish and lingcod in waters (a) between Santa Cruz

Point (Santa Cruz County) and Point Sur lighthouse in Monterey County in waters 183 m or less in depth and (b) between Point Sur lighthouse and Pfeiffer Point in Monterey County in waters 137 m or less in depth (CDFG code, Section 8692). Prior to 1997, trawlers fishing outside of state waters were only required to record the start coordinates of their trawl runs and are now mandated to record end coordinates to provide a more accurate spatial estimation of the each trawl track. Recently, (enforced Sept. 2006) the no trawl zone of three nautical miles from California's shoreline was updated to exclude trawling within Monterey Bay determined by a boundary crossing the mouth of the bay at Santa Cruz and Point Pinos (CDFG code, Section 8841(h)).

Logbook data by gear type of the total number of commercial vessels and the total number of recreational anglers onboard commercial passenger fishing vessels (also known as CPFVs or charter boats) were obtained from the California Department of Fish and Game (CDFG). Fishing locations used by commercial fishers and CPFVs were summarized spatially by fishing blocks (often referred to as 'California Trawl Blocks'). Each fishing block is 10-minutes latitude-longitude (10'x10') and forms a grid of comparable, equally sized areas for CDFG to track landing receipts over time. Additional data were collected from on-board CPFV surveys collected by CDFG observers. Like the CPFV logbook data, the CPFV observer data included the total number of recreational anglers recreational charter boats. This information was summarized by CDFG using 1-minute latitude-longitude (1'x1') microblocks. In combination with CPFV logbook data, the finer spatial resolution of the CPFV observer data provided a more accurate description of recreational fishing effort at the three study areas.

Fisheries Data Interpretation

To quantify and visualize fishing intensity by gear type, ArcMap 9.2 was used to categorize the total number of commercial vessels and the total number of recreational anglers into three relative classes (low, moderate, high) of intensity using Natural Breaks (Jenks) classification method. These classes were based on natural groupings within the data that had similar values and where there were gaps in the data. This method was used in order to find an appropriate classification for the varying ranges of vessels and anglers using each gear type (Table 3). Intensities of five bottom-contact commercial gear types were classified: bottom trawl, traps, bottom-set gillnet, bottom-set longline, and hook and line. The fishing methods used by anglers onboard CPFVs were hook and line gears (rod and reel, jig gear, etc.), so CPFV logbook and observer data were each categorized into an additional category "recreational hook and line".

Invertebrate Community and Fisheries Data Correlation

Pearson's rank correlation was used to rank and compare the observed relative abundances, absolute densities and average sizes of invertebrates to the ranked predicted levels of fishing impacts at each site. The correlation coefficient ("r") ranges from +1 to -1 and reflects the degree of linear relationship between the observations and predictions. A correlation of +1 indicates a perfect positive linear relationship between the variables.

RESULTS

Habitat Characteristics

A total of 45 submersible dives were completed at the three study sites at 19-252 m depths, in which 1,317 habitat patches that covered 6.85 hectares were surveyed (Table 4, Appendix A). The abundance (total area) of the various habitat types was unique to each site (Figure 2). At Portuguese Ledge, the greatest areas of habitat were made up of mixed and soft

substrata. No mud habitats were surveyed at Point Sur; the primary habitat types were mixed substrata, with some sand and high-relief hard rock. The largest habitat areas surveyed at Big Creek were soft sediments and hard rock, with small areas of mixed substrata. Frequencies of most habitat types stratified by depth had similar trends among sites (Appendix B). Hard and mixed rocks were most commonly found in mid-water depths (61-120 m) at Portuguese Ledge and Point Sur. This trend was also documented at Big Creek in addition to hard rock and sand surveyed in shallow water (<60 m) and hard rock with mud substrata present in deep water (>120 m). Also, Portuguese Ledge and Big Creek surveyed depths greater than 200 m that were primarily soft mud sediments.

Invertebrate Community

A total of 54,439 individual megafaunal invertebrates from 54 taxa and 9 phyla were quantified (Appendix C). The relative abundance of invertebrates from the two categories: slowgrowing, sessile and fast-growing, mobile species differed among the three sites (Table 5). At Portuguese Ledge, the greatest percent of all invertebrate observations were crinoids (19%), vermillion sea stars (13%), and sea pens (5%). Crinoids were very common at Point Sur (65%) and sponges were also frequently observed (5%). At Big Creek, sea pens and sponges comprised 11% and 7%, respectively, of all observed individuals. Also, crinoids (9%) and vermillion sea stars (7%) were found at Big Creek in similar abundances.

Densities of slow-growing, sessile invertebrates varied across habitat types at the three sites (Appendix D). Sponges were most dense on high-relief hard rock and mixed substrata. Pooled densities of the four morphologies of sponges were greatest at Point Sur (pooled mean= 14.59/100m²; SE=4.22; n=1,368) and the lowest at Portuguese Ledge (pooled mean=2.27; SE=2.03; n=70). Vase and barrel sponges were more common at Portuguese Ledge than at Big

Creek, whereas flat and foliose sponges were denser at Big Creek than Portuguese Ledge (Table 6). Gorgonians were mostly found on hard and mixed rock, and were most common at Portuguese Ledge (mean= $2.47/100m^2$; SE=1.01; n=300) with fewer present in soft sediments. Sea pens were predominately found in low-relief soft sediments. Both Portuguese Ledge and Big Creek had high densities of sea pens (mean= $3.32/100m^2$; SE=1.21; n=1,027 and mean= $3.99/100m^2$; SE=2.28; n=949 respectively).

Fast-growing and mobile species such as vermillion sea stars and crinoids were found over a wide range of habitats (Appendix D). Vermillion sea stars were observed on all 16 habitat types among sites and were most common at Portuguese Ledge (mean= $46.34/100m^2$; SE=12.33; n=2,592). In contrast, crinoid densities were variable among habitat types at the three sites, but were most dense on hard and mixed substrata. Crinoids were more abundant at Point Sur (mean= $220.58/100m^2$; SE=88.7; n=16,748) than at Portuguese Ledge and Big Creek (Table 6).

Size distribution of slow-growing and sessile species such as the four morphological groups of sponges, gorgonians, and sea pens varied among sites (Figure 3; Appendix E). Sponge sizes pooled by morphological group were significantly larger at Portuguese Ledge than at Big Creek (one-way ANOVA; *F*=3.35; df=2, 2016; p=0.035). A Kruskal-Wallis test determined the sizes of gorgonians among sites to be significantly different (*H*=66.84; df=2; p < 0.001) and overall the largest at Big Creek (mean=22 cm; SE=0.54; n=37) and smallest at Point Sur (mean=13 cm; SE=0.54; n=300). Sizes of sea pens were also found to be significantly different among sites (*H*=182.48; df=2; p < 0.001) and displayed the opposite trend of gorgonian sizes, with the overall largest sea pens at Point Sur (mean=32 cm; SE=1.99; n=127) and smallest at Big Creek (mean=19 cm; SE=0.47; n=949). The largest individual sea pens were observed at Portuguese Ledge (150 cm) and Big Creek (130 cm).

NMDS resulted in a 4-dimensional solution, with a final stress of 11 after 169 iterations, explaining 82% of the variance in the megafaunal invertebrate community. Although the stress level achieved was considered a "fair" level, the large number of sample units partly explains the high value (Kruskal & Wish 1978; McCune & Grace 2002). The solution was found to be statistically different from a randomized solution using a Monte Carlo test (p=0.01). Axis 3 (25% of the total variation) combined with Axis 2 (20% variation) explained the greatest variation of the final ordination and displayed a habitat gradient of soft sediments transitioning into mixed substrata and then to hard rock. Thus, Axes 3 and 2 primarily contrasted differences in habitats at the three sites. Portuguese Ledge was mostly soft and mixed habitats, whereas Point Sur was mixed and hard rock habitats. Big Creek displayed the most variable range of habitats, which was scattered across the ordination of all habitat types (Figure 4). These habitat patterns corresponded to the varying depth ranges surveyed at each site. Soft mud sediments are commonly found in deep waters and both Portuguese Ledge and Big Creek surveyed depths greater than 200 m. Hard and mixed rock habitats are characteristic of the mid-shallow depths, which were surveyed at all three sites.

The NMDS ordination indicated that sea pens occurred on soft sediments and gorgonians were present on mixed substrata at Portuguese Ledge and Big Creek. Sponges co-occurred on hard rock and some mixed substrata, generally at Point Sur and Big Creek. For the fast-growing, mobile species, the ordination indicated that crinoids were primarily found at Point Sur and Portuguese Ledge on mixed substrata, while vermillion sea stars were associated with hard and mixed rock at Portuguese Ledge (Figure 4).

Fishing Intensity

Among the three study sites, fishing intensity of the total number of vessels and anglers using all gear types was greatest at Portuguese Ledge (Figure 5). Trawling may have occurred over cobble and mud-sand substrata surveyed at Portuguese Ledge outside of the three nautical miles no trawl zone (Pers. Comm., J. Mason, NOAA). The use of gillnets is likely to have been over submersible dives conducted farthest from shore at depths greater than 183m (CDFG code, Section 8692). It is well known, that the recreational hook and line fishery has historically favored Portuguese Ledge and surrounding areas. The total number of recreational anglers as determined by the CPFV observer data was highest around the ports of Monterey and Pacific Grove, therefore contributing to the high number of recreational hook and line anglers within the southern fishing block at Portuguese Ledge.

The Point Sur study area had moderate to low intensity of the total number of vessels and anglers using all gear types (Figure 5). Trawling occurred in all fishing blocks beyond three nautical miles from shore, so it is likely that trawlers focused their effort on the soft sediments to the northwest of submersible dives in the western fishing block. Therefore, trawling was very light or absent over the rocky areas surveyed at Point Sur (Pers. Comm., J. Mason, NOAA).

Fishing intensity at Big Creek was low to moderate. All submersible dives were conducted within three nautical miles from the shore, so it is unlikely there was any trawling at Big Creek. However, there was a moderate use of traps and bottom-set longlines within the fishing block that included all submersible dives. Intensity of hook and line gear use was low (Figure 5).

Among the three sites, 151 incidences of derelict fishing gear were observed. Portuguese Ledge had the most gear (n=131) and had more categories of gear than was seen at either Point

Sur or Big Creek. Fishing lines, which included monofilament line, longlines, and ropes, comprised 82% (n=125) of all observed gear at Portuguese Ledge. Twice as many nets (most likely gillnets) were found at Portuguese Ledge than at Big Creek (Figure 6).

Correlation of Invertebrate Community and Fishing Intensity

The predicted levels of fishing impacts to slow-growing, sessile invertebrates corresponded to the documented levels of fishing intensity at each site, such that there would be a high impact to sponges, gorgonians, and sea pens at Portuguese Ledge, a moderate impact at Point Sur, and a low impact at Big Creek (Table 7 (a)). The ranked relative abundances of sponges among the three sites were significantly correlated with the ranked predicted fishing impact levels (r = 1.0, p < 0.001); as the least percent of all observed sponges were at Portuguese Ledge (0.3%) and the greatest percent at Big Creek (7%). However, ranked absolute sponge densities were not significantly correlated with the ranked predicted fishing impact levels among the three sites. Ranked sponge size displayed a significant negative correlation to the ranked predicted fishing impact levels (r = -1.0, p < 0.001), and the largest sponges were observed at Portuguese Ledge (22 cm) and the smallest at Big Creek (20 cm). Overall, the ranked relative abundances, absolute densities, and sizes of sponges reached a non-significant correlation to the ranked predicted levels off fishing impacts at each site. Similarly, the ranked abundances, densities, and sizes of gorgonians and sea pens were each not significantly correlated to the predicted levels of fishing impacts (Table 7 (b)).

The potential levels of fishing impacts to fast-growing, mobile invertebrate species were predicted to be moderate at Portuguese Ledge and overall low impact at Point Sur and Big Creek (Table 7 (a)). The ranked relative abundances and absolute densities of crinoids and vermillion

sea stars were not significantly correlated to the ranked predicted fishing impact levels among the three sites (Table 7 (b)).

DISCUSSION

General Patterns

The habitat characteristics and associated megafaunal marine invertebrates documented at Portuguese Ledge, Point Sur, and Big Creek exemplify central California's unique continental shelf ecosystem. Located within Monterey Bay, Portuguese Ledge is an area comprised of deepwater mud habitats and mid-water low-relief rock that was primarily covered in a fine sediment layer. Among these habitats sea pens, gorgonians and vermillion sea stars were very common. At Point Sur, a high-current area, substrata were primarily mixed and hard rock mostly associated with sponges and crinoids. Oriented along an exposed coast, Big Creek was unique to the high-surge, shallow rock-sand habitats and deep rock-mud habitats of the submarine canyons surveyed at the outer extent of the reserve. Sea pens and sponges were the most common slowgrowing, sessile invertebrates and vermilion sea stars and crinoids were also found in similar abundances at Big Creek.

The intensity of fishing activities displayed significant spatial variability among the three study sites, with high levels found at Portuguese Ledge, decreasing to Point Sur and Big Creek. Portuguese Ledge was by far the most heavily fished area of the three study sites. This pattern was supported by the majority (87%) of observations of derelict fishing gear. However, the large spatial scale of fishing intensity within the 10'x10' fishing blocks may have been misleading, especially when describing fishing at Portuguese Ledge. The two eastern near-shore fishing blocks that encompassed Portuguese Ledge submersible dives also incorporated Monterey and Carmel Canyons. When near-shore stocks declined, Monterey fishing fleets expanded their effort

to deeper and more remote areas such as submarine canyons, which could explain why the two eastern fishing blocks displayed high intensity of traps and bottom-set gillnets and a moderate use of bottom-set longlines and trawling (Mason, 1995). Nonetheless, Portuguese Ledge has historically been a favored spot for the hook and line and other fisheries, due to its accessibility from the ports of Monterey and Moss Landing (Pers. Comm., J. Mason, NOAA).

Overall, Point Sur experienced a moderate level of fishing intensity compared to Portuguese Ledge most likely because this fishing spot is more exposed to weather and requires longer travel time for vessels coming from ports within Monterey Bay. Fishing intensity was low at Big Creek both because this area is far from fishing ports (90 km from Monterey and 120 km from Morro Bay) and designated an ecological reserve, so any fishing should have occurred outside of the reserve boundaries. There was a moderate usage of traps, which are most likely targeting spot prawns in the submarine canyons outside of the reserve's boundaries. The low fishing intensity documented at Big Creek is consistent with the correspondence analysis that resulted in no difference of invertebrates inside and outside the reserve. Also, Big Creek is a relatively new reserve and was closed to fishing three years prior to the submersible surveys.

Influences to the Invertebrate Community

Sponges were primarily found on high-relief rock and mixed substrata at all sites, corresponding to Tissot et al. (2006) sponge-habitat observations on the continental shelf off southern California. Trawl gear outfitted with roller gear could potentially be dragged over sponges living on low-relief mixed rock habitats and cause the direct removal of these sessile invertebrates. In areas of high-relief hard substrata, longline, gillnet, and hook and line gear could snag on sponges removing or breaking them. The relative abundance of sponges followed the predicted levels of fishing impacts among sites; however the average ranked abundances,

densities and sizes of sponges were not significantly correlated to the predicted levels of fishing impacts. Considering the large area of hard and mixed rock surveyed at Point Sur (1.27 hectares), it was not surprising that all sponge groups were most abundant at this site. Although, there was the possibility of bottom trawling over sponges at Point Sur, the rugosity of the habitat may have deterred trawlers from fishing in this area, focusing their effort over the soft sediments found to the northwest of the surveyed area. Also, upwelling events at Point Sur are ideal for successful recruitment and settlement of sessile, filer-feeding invertebrates such as sponges.

Despite the high intensity of fishing at Portuguese Ledge with longline, gillnet, and hook and line gear, sizes of sponges were not smaller than those at the other sites, which would have been predicted by these gears contacting high-relief rock habitats, snagging and breaking sponges. In fact, average sponge size reached a negative correlation to the predicted fishing impact levels. The overall larger sizes of sponges at Portuguese Ledge may have been due to the natural protection provided by Monterey Bay, unlike high-current, exposed areas like Point Sur and Big Creek.

Gorgonians displayed a similar habitat distribution as sponges on hard and mixed rock. Tissot et al. (2006) also observed gorgonians in mixed cobble-boulder habitats in southern California at 144-163 m depth. The gorgonians grouped with soft sediments in the NMDS ordination are likely to have been attached to hard substrata hidden beneath a thick mud cover. Therefore, gorgonians on low-relief mixed and soft sediment could be removed by bottom trawls and/or crushed and snagged by active traps. Like sponges in high-relief rock habitats, gorgonians could become entangled in longlines, gillnets, and hook and line gear resulting in their removal or decreased size. The abundance of gorgonians was notably greatest at Portuguese Ledge and sparse at Big Creek, which was supported by a non-significant correlation of observed

abundances to the predicted levels of fishing impacts. Factors other than fishing intensity were likely influencing the distribution of these soft corals. For example, the ranges of depth varied among sites, which may be the major indicator of gorgonian distribution. Big Creek included the greatest range of depths (19-249 m) and gorgonians were found here among 50-174 m. On the other hand, the depth range at Portuguese Ledge and Point Sur was primarily shallower and possibly more favorable to gorgonians (Lamb and Hanby, 2005), which may be why higher gorgonian densities occurred at these sites. Although a non-significant correlation of average gorgonian size and the predicted levels of fishing impacts was reached, gorgonians at Big Creek were overall larger than those at Portuguese Ledge. It could be that Big Creek gorgonians were older or grow faster than those at Portuguese Ledge, indicating less impact of fishing gear at Big Creek and possibly past fishing disturbances at Portuguese Ledge. Further, monofilament fishing line was observed tangled around gorgonians at Portuguese Ledge, so it may be possible that hook and line anglers are snagging gorgonians with their gear.

Hixon and Tissot (2007) documented that sea pens were highly vulnerable to ground fishing activities, specifically bottom trawling on soft sediments of Oregon's continental shelf. Sea pens were also observed on soft sediments in this study, which made them vulnerable to removal, crushing and snagging by bottom trawl gear and traps. Despite the differences in the potential level of trawling and trap use, sea pen abundance and size were not significantly correlated with the predicted levels of fishing impacts among sites and had similar densities at Big Creek and Portuguese Ledge. Overall, the high frequency of soft mud habitats surveyed at these sites may have contributed to sea pen abundance. However, the effects of fishing gear may have been responsible for observations of broken sea pens on the seafloor. The most damaged sea pens were at Portuguese Ledge (about 2% of total individuals), of which 88% ranging in size

of 30-100 m were found damaged on submersible dives outside of the three nautical mile no trawl zone.

Dense aggregations of crinoids were documented on mixed substrata and vermillion sea stars occurred on high-relief and mixed rock habitats. Due to the mobile and fast-growing nature of these invertebrates, it was predicted that trawling in low-relief mixed habitats would result in temporary displacement if they are not removed in the net. Further, if longlines, gillnets, and hook and line gear became entangled on high-relief rock, displacement of crinoids and vermillion sea stars could occur during gear retrieval. Yet, the overall impact level of these gear types would be low.

Generally vermillion sea stars were common at all sites, supported by the non-significant correlation of abundance measures and predicted levels of fishing impacts. Vermillion sea stars were most abundant at Portuguese Ledge and in addition to large areas of mud substrata surveyed in this area, detritus and sediment cover over rocks may have served as a food source to these sea stars. Previous studies on the impacts of bottom trawling to invertebrates have noted that mobile sea stars were resistant to trawl disturbance (e.g. Freese et al., 1999; Hixon and Tissot, 2007). Also, the high frequency of hook and line gear at Portuguese Ledge did not appear to have an impact on vermillion sea star abundance as predicted.

Crinoids were also common among the three sites, resulting in a non-significant correlation of overall abundance to the predicted levels of fishing impacts. However, crinoids were remarkably the densest at Point Sur on low-relief mixed substrata. The strong currents, upwelling events, and ample mixed substrata characteristic of Point Sur made this site an ideal environment for the success of this filter feeding species. Potential displacement of crinoids due to trawling and hook and line gear at Point Sur as well as the other two sites was minimal.

Therefore, the distribution of vermillion sea stars and crinoids was widespread among the three sites and perhaps was due to the combination of ideal environmental conditions and the resilience of these fast-growing and mobile species to fishing disturbance.

Conclusions

The three sites of focus for this study varied in fishing intensity, yet it appeared that environmental conditions were influencing the abundance and distribution of megafaunal marine invertebrates. One of the most challenging aspects of determining the impacts of fishing intensity on megafaunal invertebrates was the lack of high resolution data on the distribution of fishing effort. Yet, despite the inability to identify direct fishing impacts to invertebrates, the unique approach of this study can be applied to other areas on the continental shelf that are being influenced by bottom-contact fishing gear, therefore contributing to fisheries management regulations. Also, the true value of this work is that before now, there had been no previous documentation of megafaunal marine invertebrates at Portuguese Ledge, Point Sur and Big Creek.

A more beneficial approach in determining the differential influences of environmental variables and fishing impacts to megafaunal marine invertebrates would be to use manipulative or before-after impact studies. Specifically, there is a suite of new marine protected areas (MPAs) along California's central coast (Pigeon Point to Point Conception). The 29 MPAs function as part of an overall statewide network of MPAs currently being developed and include "no take" state marine reserves (SMR), state marine conservation areas (SMCA) and state marine parks (SMP). Multiyear monitoring of the deepwater invertebrate and fish communities inside and outside of eight of the newly formed SMRs and SMCAs (including Portuguese Ledge, Point Sur and Big Creek) is currently being conducted to evaluate the effectiveness of the new

MPAs (Yoklavich et al., 2008). These longitudinal studies are important to assess the density, diversity, size composition and health of slow-growing, long-lived megafaunal invertebrates and fishes within the MPAs. The historical data from this study will also contribute to the baseline analysis of the invertebrates that are now protected from recreational and commercial harvest in these areas. It is important to identify areas containing high abundances of gorgonians, sponges, and other megafaunal marine invertebrates for the important ecological roles they serve in contributing to biodiversity and habitat.

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Invertebrate Categories	Indicator Taxa	Biological Characteristics	Impacts of Fishing Gear
Slow-Growing, Sessile	Sponges (Porifera) Gorgonians (Gorgonacea) Sea Pens (Subselliflorae)	Calcareous or siliceous skeletons makes these invertebrates structurally rigid, sessile, slow- growing, long-lived; they exhibit complex morphology and large sizes	 <i>Trawl Gear:</i> Removal, crushing, burying, and breaking <i>Pots/Traps:</i> Crushing and snagging with settling and hauling gear <i>Bottom-set longlines and gillnets:</i> Entangling and removal during gear retrieval <i>Hook and line:</i> Snagging and breaking from sinkers and monofilament line
Fast-Growing, Mobile	Sea stars (Asteroidea) Crinoids (Florometra serratissima)	Endoskeleton is composed of calcium carbonate crystals imbedded in soft tissues; tube feet (podia) allow for movement and individuals often aggregate in high numbers	 <i>Trawl Gear:</i> Removal or temporary displacement and burying <i>Pots/Traps:</i> Crushing or temporary displacement with settling and hauling gear <i>Bottom-set longlines and gillnets:</i> Removal or temporary displacement during gear retrieval <i>Hook and line:</i> Possible temporary displacement from sinkers and monofilament line

Table 1. Biological characteristics and fishing gear impacts to two categories of megafaunal marine invertebrates.

Table 2. Bottom-contact fishing gear types used in central California and their potential levels of impact to two categories of invertebrates: slow-growing, sessile species and fast-growing, mobile species as determined by disturbance components of each gear type. Components of fishing gear disturbance and potential levels of impact to invertebrates are based on a synthesis of previous findings summarized from Morgan and Chuenpagdee, 2003 and Hourigan et al., 2007. * denotes if gear were to be dragged long distances during retrieval

Disturbance Components of Fishing GearFishing Gear				nts of	Potential Levels of Impact to Invertebrates		
		Magnitude	Areal Extent	Frequency	Slow-Growing; Sessile Species	Fast-Growing; Mobile Species	
Bottom/Otter	r Trawl	High	High	High	High	Medium	
Turne	Single-set traps	Medium [*] -Low	Medium [*] -Low	Low	Malian	Lore	
Traps	Longline traps	High [*] -Medium	High [*] -Medium	Medium	Medium	Low	
Bottom-set L	ongline	Medium [*] -Low	Medium [*] -Low	Medium	Medium	Low	
Bottom-set G	illnet	Medium [*] -Low	Medium [*] -Low	Medium	Medium	Low	
Hook and Lin	ne	Low	Low	High	Medium-Low	Low	

Table 3. Ranges of total number of vessels and anglers using five gear types in central California over a six year period (1993-1998).
Impact scale was determined using ArcMap 9.2 natural breaks classification method.

	Bottom Trawl	Traps	Bottom-set Gillnet	Bottom-set Longline	Hook & Line: Commercial	Hook & Line: Recreational	Hook & Line: CPFVobserver
Impact Scale	No. Vessels	No. Vessels	No. Vessels	No. Vessels	No. Vessels	No. Anglers	No. Anglers
Low	0-9	0-7	0-4	0-16	0-108	0-6,006	0-151
Moderate	10-31	8-20	5-17	17-66	109-472	6,007-18,957	152-453
High	32-121	21-53	18-49	67-231	473-1,376	18,958-53,804	454-1,169

Table 4. Number of submersible dives, depth ranges, number of habitat patches, and area surveyed at Portuguese Ledge, Point Sur and Big Creek study sites.

Study Site	No. of Dives	No. of Habitat Patches	Area (h)	Depth range (m)
Portuguese Ledge	11	311	2.08	71-252
Point Sur	6	373	1.71	72-126
Big Creek	28	633	3.06	19-249
Total	45	1,317	6.85	19-252

Table 5. Relative abundance (percent of total observations) of slow-growing, sessile and fastgrowing, mobile invertebrates at Portuguese Ledge, Point Sur and Big Creek study sites.

Invertebrate Categories	Relative Abundance % total observations					
	Portuguese Ledge	Point Sur	Big Creek			
Slow-growing, sessile						
Sponges (Porifera)	0.3%	5%	7%			
Gorgonians (Gorgonacea)	1%	0.2%	0.4%			
Sea Pens (Subselliflorae)	5%	0.5%	11%			
Fast-growing, mobile						
Vermillion Sea Star (Mediaster aequalis)	13%	3%	7%			
Crinoids (Florometra serratissima)	19%	65%	9%			

Table 6. Mean density $(no./100m^2)$ of slow-growing, sessile and fast-growing, mobile megafaunal marine invertebrate taxa found at Portuguese Ledge, Point Sur and Big Creek study sites. SE is standard error and *n* is the total number of observations per taxon.

	Portu	iguese Ledg	ge	F	oint Sur		F	Big Creek	
Invertebrate Categories	Densi	ty (no./100m	n ²)	Densit	ty (no./100r	m ²)	Densi	ty (no./100m ²	2)
	Mean	SE	n	Mean	SE	n	Mean	SE	n
Slow-growing, sessile									
Sponges (Porifera)									
Flat	0.80	0.76	11	9.83	2.20	901	1.57	0.72	240
Foliose	0.49	0.36	24	2.81	1.04	248	2.74	1.05	283
Barrel	0.76	0.73	28	2.11	0.87	195	0.14	0.06	50
Vase	0.22	0.18	7	0.16	0.11	24	0.03	0.03	8
Gorgonians (Gorgonacea)	2.47	1.01	300	1.16	0.70	59	0.28	0.24	37
Sea Pen (Subselliflorae)	3.32	1.21	1,027	1.03	0.50	127	3.99	2.28	949
Fast-growing, mobile	Fast-growing, mobile								
Vermillion Sea Star (Mediaster aequalis)	46.34	12.33	2,592	10.18	2.93	667	14.59	6.53	625
Crinoids (Florometra serratissima)	108.30	79.04	3,777	220.58	88.70	16,748	11.09	6.45	748

Table 7(a). Predicted levels of fishing impacts to the two categories of invertebrates at Portuguese Ledge, Point Sur and Big Creek. Ranked level is identified by ().

Site	Predicted Levels of Impact to Invertebrates				
Site	Slow-growing, sessile taxa	Fast-growing, mobile taxa			
Portuguese Ledge	High (3)	Moderate (2)			
Point Sur	Moderate (2)	Low (1)			
Big Creek	Low (1)	Low (1)			

Table 7(b). Observed abundance, density and size of each taxon among the three sites. Ranked level is identified by (). The final Pearson's correlation coefficient (r) is the overall ranked observed measures correlated to the ranked predicted impact levels from table 7(a).

Observations	Site	Slow-growing, sessile taxa			Fast-growing, mobile taxa			
		Sponges	Gorgonians	Sea Pens	Crinoids	Vermillion Stars		
	Portuguese Ledge	0.3 (3)	1 (1)	5 (2)	19(1)	13 (1)		
% of total Obs.	Point Sur	5 (2)	0.2 (3)	0.5 (3)	65 (1)	3 (2)		
	Big Creek	7 (1)	0.4 (2)	11 (1)	9 (2)	7 (1)		
Density/100m2	Portuguese Ledge	2 (3)	2 (1)	3 (2)	108 (1)	46 (1)		
	Point Sur	15 (1)	1 (2)	1 (3)	220 (1)	10 (2)		
	Big Creek	4 (2)	0.2 (3)	4 (1)	11 (2)	15 (1)		
Size (cm)	Portuguese Ledge	22 (1)	17 (2)	27 (2)				
	Point Sur	21 (2)	13 (3)	32 (1)	Not Sized			
	Big Creek	20 (3)	21 (1)	19 (3)				
Average Pearson Correlation (r) of Observations and Predictions		0.5	-0.5	0.5	-0.5	-0.5		





Figure 2. Total area of each substratum type in the three habitat categories (hard, mixed, soft) at Portuguese Ledge, Point Sur and Big Creek study sites.





Figure 3. Mean size (cm) of slow-growing, sessile megafaunal marine invertebrate taxa found at Portuguese Ledge, Point Sur and Big Creek study sites. SE is standard error. * Significantly different (ANOVA; P<0.05)



Figure 4. Nonmetric Multidimensional Scaling ordination of habitat, study sites and megafaunal marine invertebrates in central California.



Figure 5. Distribution of fishing intensity over a six year period (1993-1998) by five bottom-contact gear types used in central California. Relative impact scale was determined using ArcMap 9.2 natural breaks of total number commercial vessels fishing trawls, traps, gillnets, longlines, hook and line, and total recreational anglers (including CPFV observer) using hook and line gear. Impact scale: yellow-low; orange-moderate; red-high (range of impact scale for each gear type is defined in Table 3)



Hook and Line: Recreational



Hook and Line: CPFV observer



Figure 5. continued



Figure 6. Number of derelict fishing gears observed per area (hectares) surveyed at Portuguese Ledge, Point Sur and Big Creek study sites.



Appendix A. Number of habitat patches in each substratum type at Portuguese Ledge, Point Sur and Big Creek study sites.

Appendix B. Percent area of the three habitat categories (hard, mixed, soft) stratified by depths at Portuguese Ledge, Point Sur and Big Creek study sites.



Appendix C. Number of observations and percent of total observations for invertebrates identified at Portuguese Ledge, Point Sur and Big Creek study sites.

Phylum	Таха	Portuguese Ledge		Point Sur		Big Creek	
		# of Obs.	% of Total Obs.	# of Obs.	% of Total Obs.	# of Obs.	% of Total Obs.
Porifera	flat sponge	11	0.05	901	3.5	240	2.76
	foliose sponge	24	0.12	248	0.96	283	3.25
	barrel sponge	28	0.14	195	0.76	50	0.57
	vase sponge	7	0.03	24	0.09	8	0.09
	mound sponge	1	< 0.01	1	< 0.01	23	0.26
	branching sponge			19	0.07		
Cnidaria	Subselliflorae sea pen	1,027	5.13	127	0.5	949	10.91
	Metridium farcimen	258	1.29	4	0.02	408	4.69
	Gorgonacea	300	1.50	59	0.23	37	0.43
	Urticina piscivora					160	1.84
	Stomphia coccinea	69	0.34	1	< 0.01	35	0.4
	unknown sand anemone					72	0.83
	Urticina sp.			2	< 0.01	69	0.8
-	Ptilosarcus gurneyi	20	0.10			15	0.17
	sea fan	9	0.04	4	0.02		
	unknown anemone	8	0.04			1	< 0.01
-	unknown coral					2	0.02
	Anthopleura spp.					1	< 0.01
Annelida	Serpula spp.			1	< 0.01	10	0.11

Mollusca	Octopus spp.					7	0.08
	Pleurobranchea californica			2	< 0.01		
	<i>Dorididae</i> sp.					1	< 0.01
Arthropoda	Pandalus platyceros	9	0.04			994	11.43
	Munida quadrispina					848	9.75
	Loxorhynchus crispatus	1	< 0.01	13	0.05	1	< 0.01
	hermit crab					6	0.07
	unknown crab spp.					2	0.02
	<i>Cancer</i> spp.					1	< 0.01
	Lopholithodes foraminatus					1	< 0.01
Bryozoa	Heteropora pacifica					184	2.11
Brachiopoda	Laqueus californicus	8,357	41.76	5,750	22.35		
Echinodermata	Florometra serratissima	3,777	18.87	16,748	65.1	748	8.6
	Mediaster aequalis	2,592	12.95	667	2.6	625	7.18
	Ophiuridae	2,974	14.86	2	< 0.01	430	4.94
	Asterina miniata	6	0.03			1,887	21.69
	Lytechinus anamesus			681	2.65		
	Ceramaster patagonicus	4	0.02	222	0.86	26	0.3
	Pycnopodia/Rathbunaster	170	0.85	1	< 0.01	74	0.85
	Asterina miniata/Mediaster aequalis					221	2.54
	Parastichopus californicus	177	0.88			5	0.06
	Luidia foliolata	67	0.33	22	0.09	33	0.38
	Henricia spp.	12	0.06	10	0.04	66	0.76
	Stylasterias forreri	44	0.22			32	0.37
	Gorgonocephalus eucnemis	49	0.24			6	0.07
	Parastichopus spp.					39	0.45

Total Taxa		31		28		49	
Sum		20,014	100	25,725	100	8,700	100
Chordata	Urochordata spp.					3	0.03
	Dermasterias imbricata					1	< 0.01
	Stylasterias forreri/Orthasterias koehleri					1	< 0.01
	Linckia columbiae			1	< 0.01		
	Pteraster tesselatus	2	< 0.01	3	0.01		
	Leptasterias spp.					7	0.08
	Pisaster spp.					15	0.17
	Pteraster militaris	1	< 0.01	9	0.03	9	0.1
	Orthasterias koehleri					22	0.25
	unknown sea star spp.	10	0.05	8	0.03	9	0.1
	Pisaster brevispinus					33	0.38

Appendix D. Mean density $(no./100m^2)$ of megafaunal marine invertebrates in habitat patches of each substratum type at Portuguese Ledge, Point Sur and Big Creek study sites. Vertical bars and \pm one standard error and *n* is total number of observations per taxon.



Flat Sponges

Foliose Sponges



Barrel Sponges







Gorgonians





Sea Pens















Appendix E. Size distribution of slow-growing, sessile megafaunal marine invertebrates at Portuguese Ledge, Point Sur and Big Creek study sites.

Flat Sponges



Foliose Sponges



Barrel Sponges



Vase Sponges



Gorgonians



Sea Pens

